

NICKEL ACCUMULATION BY SERPENTINE SPECIES OF
STREPTANTHUS (BRASSICACEAE): FIELD AND
GREENHOUSE STUDIES

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ABSTRACT

Hyperaccumulation of nickel by higher plants ($>1000 \mu\text{g/g}$ in tissue) is closely associated world-wide with serpentine soils. In North America, nine hyperaccumulators have been identified, some from analysis of herbarium samples. *Streptanthus polygaloides*, found earlier to be a hyperaccumulator on Sierra Nevada serpentines, merited further study. We report on field-collected samples and greenhouse cultures of this and other *Streptanthus* species. Fresh samples from eight serpentine sites all had more than $1000 \mu\text{g/g}$ of nickel ($2430\text{--}18600 \mu\text{g/g}$), clearly confirming the earlier results. Other serpentine *Streptanthus* spp., collected in the field or grown on serpentines in the greenhouse, had modest nickel levels and could be termed excluders. Greenhouse cultures of *S. polygaloides* on non-native serpentine soils also accumulated nickel in excess of $1000 \mu\text{g/g}$. Although field samples of *S. barbiger*, a Coast Range serpentine endemic, took up low amounts of nickel, this species grown on non-native serpentine soils accumulated nickel ($69\text{--}1200 \mu\text{g/g}$). This unusual result is discussed as are the ecological and evolutionary implications of nickel accumulation and nickel exclusion in *Streptanthus*.

Exceptional uptake of nickel by a small proportion of the plant species found on serpentine soils (derived from serpentinites and related ultramafic rocks) is now known to occur in many parts of the world. Nearly 200 species are known, in at least some of their occurrences, to contain more than $1000 \mu\text{g/g}$ Ni (dry weight basis), a level that has been set as the threshold for applying the term 'hyperaccumulation' (Brooks et al. 1977). The most recent comprehensive list of plant species exhibiting this behavior is that of Reeves (1992).

Serpentines occur in North America, both on the eastern seaboard from Georgia to Quebec and Newfoundland, and on the Pacific coast (California, Oregon, Washington, and British Columbia). Despite this rich display, and the occurrence of over a thousand plant species on North American serpentine soils, only nine taxa have been reported to exhibit nickel hyperaccumulation: *Streptanthus polygaloides* Gray (Reeves et al. 1981), three varieties of *Thlaspi montanum*

TABLE 1. RECORDS OF NICKEL HYPERACCUMULATION IN NORTH AMERICAN PLANTS.

Species	Locality	Nickel conc. ($\mu\text{g/g}$ dry wt.)	Reference
Asteraceae			
<i>Senecio pauperculus</i>	W. Newfoundland	1903	Roberts (1992)
<i>Solidago hispida</i>	W. Newfoundland	1023	Roberts (1992)
Brassicaceae			
<i>Streptanthus polygaloides</i>	California	1100–16,400	Reeves et al. (1981)
<i>Thlaspi montanum</i> var. <i>californicum</i>	Humboldt Co., Calif.	3850–11,600	Reeves et al. (1983)
var. <i>montanum</i>	California, Oregon, Washington	784–11,300	Reeves et al. (1983)
var. <i>siskiyouense</i>	Josephine Co., Ore- gon	3920–27,800	Reeves et al. (1983)
Caryophyllaceae			
<i>Arenaria humifusa</i>	W. Newfoundland	2330	Roberts (1992)
<i>A. marcescens</i>	W. Newfoundland	2365	Roberts (1992)
<i>A. rubella</i>	Skagit Co., Washing- ton	1360	Kruckeberg et al. (1993)

L. (Reeves et al. 1983), three species of *Arenaria* (Roberts 1992; Kruckeberg et al. 1993) and two composites, *Senecio pauperculus* and *Solidago hispida* (Roberts 1992). Relevant data are summarized in Table 1.

The discovery of *Streptanthus polygaloides* as a hyperaccumulator occurred during a larger survey of California serpentine plants (Reeves et al. 1981), in which special attention was paid to *Streptanthus* because nearly all the twelve species in subgenus *Euclisia* are serpentine endemics (Kruckeberg and Morrison 1983). However, *S. polygaloides* was unique in the genus for its nickel-accumulating propensity, the concentrations being approximately 100 times greater than in the other serpentine species.

The initial study was based on the analysis of small samples of tissue taken from herbarium specimens, which has been useful as an exploratory tool in the investigation of nickel accumulation in other serpentine floras (Brooks et al. 1977). The present study was designed to extend the earlier work by obtaining and analyzing fresh field-collected samples of *Streptanthus* species together with soil samples from the same sites, and to investigate the behavior of various *Streptanthus* species grown under greenhouse conditions on

TABLE 2. LOCATION OF FIELD SPECIMENS OF *STREPTANTHUS* AND ASSOCIATED SOILS. ^a Kruckeberg's field numbers.

Sam- ple no. ^a	Species	Location
6732	<i>S. polygaloides</i> A. Gray	Nevada Co., Washington Rd., 1.7 mi N of Route 20
6734	<i>S. polygaloides</i> A. Gray	Placer Co., S shore of Sugar Pine Reservoir, 8 mi E of Iowa Hill
6735	<i>S. polygaloides</i> A. Gray	Placer Co., 1.1 mi SW of Garden Valley
6736	<i>S. polygaloides</i> A. Gray	Calaveras Co., Route 49, 3 mi N of San Andreas
6737	<i>S. polygaloides</i> A. Gray	Tuolumne Co., Redhill Rd., 2.5 mi SW of Chinese Camp
6738	<i>S. polygaloides</i> A. Gray	Tuolumne Co., Route 49, 5.8 mi N of Coulterville
6739	<i>S. polygaloides</i> A. Gray	Mariposa Co., Route 49, 5.1 mi S of Coulterville
6740	<i>S. polygaloides</i> A. Gray	Mariposa Co., Route 49, 8.5 mi S of Coulterville
6741	<i>S. tortuosus</i> Kellogg	Mariposa Co., Route 49, 8.5 mi S of Coulterville
6742	<i>S. breweri</i> A. Gray	Napa Co., 0.5 mi on Berryessa-Knoxville Rd. from Route 128
6752	<i>S. breweri</i> A. Gray	Lake Co., Hill 1030, 4 mi NE of Middletown
6743	<i>S. hesperidis</i> Jepson	Lake Co., Rabbit Hill reserve, Middletown
6750	<i>S. hesperidis</i> Jepson	Lake Co., Hill 1030, 4 mi NE of Middletown
6744	<i>S. barbiger</i> E. Greene	Lake Co., Sulfur Cr. Rd.
6745	<i>S. barbiger</i> E. Greene	Lake Co., Sulfur Cr. Rd.
6746	<i>S. barbiger</i> E. Greene	Lake Co., S of junction, Routes 29 & 175
6748	<i>S. barbiger</i> E. Greene	Lake Co., Socrates Mine Rd.
6756	<i>S. barbiger</i> E. Greene	Mendocino Co., Feliz Cr. Rd., 0.8 mi W of Hopland
6757	<i>S. barbiger</i> E. Greene	Mendocino Co., Hopland-Yorkville Rd., 6.3 mi W of Hopland
6749	<i>S. morrisonii</i> F. W. Hoffm.	Napa Co., Butts Cr. Canyon, 1 mi E of county line
6751	<i>S. glandulosus</i> Hook.	Lake Co., Hill 1030, Middletown
6755	<i>S. glandulosus</i> Hook.	Mendocino Co., Mountain House Rd., 2.5 mi S of Hopland

serpentine and non-serpentine soils. We wished to probe such questions as the following: (i) do all populations of *S. polygaloides* exhibit nickel hyperaccumulation? (ii) do the nickel concentrations in field specimens of various *Streptanthus* species approximate those of the herbarium samples previously analyzed? (iii) how closely does the nickel-accumulating behavior under greenhouse conditions resemble that in the field? (iv) what happens to *S. polygaloides* when it is grown on non-serpentine soil?

Accordingly, in May 1988 we collected living plants from serpentine sites in the western foothills of the Sierra Nevada. Besides sampling eight populations of *S. polygaloides* there, we collected 14 other samples of 6 other *Streptanthus* species from serpentine sites in the Sierra Nevada and the Coast Ranges of California. Table 2 lists the locations and the taxa sampled.

Greenhouse experiments were carried out with seed of four species, *S. polygaloides*, *S. barbiger*, *S. insignis* and the non-serpentine *S. heterophyllus* Nutt., using four serpentine soils from California and Washington as well as a greenhouse compost soil.

MATERIALS AND METHODS

Field sampling. Three to five whole plants were harvested and stored in paper bags, and air-dried prior to analysis, which was carried out on the above-ground portion of the plants only. Herbarium voucher specimens (Kruckeberg 6732-6757) were also taken. A quick, semiquantitative test for nickel hyperaccumulation was made in the field by crushing leaf tissue onto a filter paper previously impregnated with a 1% ethanolic solution of dimethylglyoxime, which forms a red nickel complex, easily visible when the nickel concentration of the tissue is equivalent to more than 1000 $\mu\text{g/g}$ on a dry weight basis. At each site a soil sample was taken from a depth of 2–10 cm; the soils were oven-dried, sieved to remove material > 2 mm and then ground to –100 mesh (<150 μm) for analysis.

Greenhouse procedures. The origins of the seed and soils used in the greenhouse tests are summarized in Table 3. Seeds of each of the four species were sown, as a mixture, on the surface of each soil type; two 6" plastic pots were used for each soil type. Since the four species are readily distinguishable both as seedlings and as flowering plants, there was no difficulty in recognition. Pots were subirrigated regularly with distilled water. Germination rates were high for all taxa; no attempt was made to count the seedlings. In some cases crowding of seedlings may have inhibited their growth. Plants were harvested in three phases, described as young, intermediate and mature (approximately 4, 7 and 10 weeks, respectively, after germination). In the mature stage, plants of all taxa were in flower or in late bud. Samples of plants and soils were treated in the same way as the field samples prior to chemical analysis.

Chemical analysis. Plant tissue (pooled for each collection number) samples were weighed into borosilicate glass test tubes which were placed in a muffle furnace. The temperature was raised to 500°C over a 2-hour period and maintained at this level overnight. After cooling, the ash was dissolved in 2 M HCl and the solutions were analyzed for nickel by atomic absorption, using the spectral line at 232.0 nm. The volume of HCl used varied between 1.0 and 20.0

TABLE 3. SOILS AND *STREPTANTHUS* SEED USED IN GREENHOUSE TESTS.

Soil no.	Nature and origin
1	Serpentine, from chaparral, Hill 1030, 4 mi NE of Middletown, Lake Co., CA
2	Serpentine, from barren talus, Newell Mine, King Cr., Chelan Co., WA
3	Serpentine, site with grasses/forbs, Newell Mine, King Cr., Chelan Co., WA
4	Dunite outcrop, Olivine Bridge, S Fork of Nooksack R., Skagit Co., WA
5	Greenhouse compost/loam, Univ. of Washington greenhouse
Seed species	Origin
<i>S. polygaloides</i>	Serpentine, 2.5 mi N of Bagby, Mariposa Co., CA
<i>S. barbiger</i>	Serpentine, hills above Cobb Valley, Glenbrook, Lake Co., CA
<i>S. insignis</i>	Serpentine talus, roadcut 6 mi W of Panoche Pass, San Benito Co., CA
<i>S. heterophyllus</i>	Granitic soil, disturbed chaparral, N of Escondido, San Diego Co., CA

ml, depending on the weight of sample taken and on the species. [Greater dilutions were used for *S. polygaloides* because of the higher nickel concentrations expected.] Several of these solutions were analyzed for a wide range of elements by inductively coupled plasma emission spectroscopy (ICP).

Soil samples (0.10–0.12 g) were digested in polypropylene beakers with 10 ml of 1:1 HF/HNO₃ mixture, evaporated to dryness and the residue taken up with 10 ml of 2 M HCl. After warming to assist dissolution, the solution volume was restored to 10.0 ml with deionized water. Samples of 2.0 ml were then diluted to 8.0 ml for analysis by ICP, this dilution being dictated by the need to keep the iron

TABLE 4. ANALYSES OF FIELD SAMPLES OF SERPENTINE *STREPTANTHUS* SPECIMENS. (Concentrations in $\mu\text{g/g}$ unless otherwise indicated.) * No. of populations sampled in parentheses.

Species ^a	Element concentrations (dry weight basis)					
	Al	Ca (%)	Co	Cr	Cu	Fe
<i>S. polygaloides</i> (8)	81–412	0.58–2.10	21–83	2–59	3–11	91–1806
<i>S. tortuosus</i> (1)	43	0.72	5	8	4	130
<i>S. breweri</i> (2)	35–54	0.99–1.60	<1	1–2	3–4	78–121
<i>S. hesperidis</i> (2)	26–54	0.55–0.66	<1	1–2	4	71–92
<i>S. barbiger</i> (6)	24–85	0.29–1.39	<1–2	1–5	3–11	84–261
<i>S. morrisonii</i> (1)	19	0.92	1	2	2	98
<i>S. glandulosus</i> (2)	35–57	0.56–1.52	<1	2	3–7	139–260

concentrations below the 500 $\mu\text{g}/\text{ml}$ level representing the upper limit of the ICP working range.

RESULTS

Field samples. The results for the ICP analyses of the field samples are shown in Tables 4 (plants) and 5 (soils). All eight population samples of *S. polygaloides* exhibited hyperaccumulation of nickel. Furthermore, in only two cases were the Ni concentrations below 10,000 $\mu\text{g}/\text{g}$ (nos. 6738, 6740), and these corresponded to soils showing the least extreme chemical characteristics of serpentine, i.e., soils 6738 and 6740 had the lowest concentrations of Mg, Fe and Ni, and the highest concentrations of K, Na and Al, indicative of mixing with some non-ultramafic material. Nevertheless, even here, the soil Ni was still above 1000 $\mu\text{g}/\text{g}$, and the plant samples contained 7000 and 2430 $\mu\text{g}/\text{g}$ Ni respectively.

All the other serpentine-endemic *Streptanthus* species contained only 4–22 $\mu\text{g}/\text{g}$ Ni, values similar to, or lower than, those reported in the herbarium survey of Reeves et al. (1981).

The cobalt levels in *S. polygaloides* are also noteworthy. It is rare for plants, even on serpentines, to contain more than 5 $\mu\text{g}/\text{g}$ of this element, although higher levels of Co (e.g., 10–200 $\mu\text{g}/\text{g}$) have occasionally been reported in Ni hyperaccumulators (Kersten et al. 1979; Kruckeberg et al. 1993).

With respect to the other elements shown in Table 4, there were no other major abnormalities, and no remarkable differences between *S. polygaloides* and the other species.

Greenhouse samples. The behavior of *S. polygaloides* as a nickel hyperaccumulator is strikingly confirmed. When grown on serpentine soils from sites where the species is not native, the plants consistently accumulated high levels of nickel (Table 5). When grown on a non-serpentine "background" soil (greenhouse potting mix), *S. polygaloides* plants had very low nickel levels (5–39 $\mu\text{g}/\text{g}$). All the

TABLE 4. EXTENDED.

Element concentrations (dry weight basis)						
K (%)	Mg (%)	Mn	Na	Ni	P	Zn
1.27–2.72	0.57–1.30	44–225	658–1476	2430–18,600	1760–4420	17–95
1.20	1.13	146	665	12	2450	48
1.77–2.68	1.58–2.30	69–106	520–566	7–13	3440–4510	27–32
0.88–1.06	2.15–2.25	55–67	303–401	19–22	3750–11,790	78–110
0.86–1.75	1.39–3.74	52–207	194–602	4–21	1680–5510	13–93
0.67	1.43	101	300	5	1040	29
1.22–1.74	0.94–1.27	24–28	661–737	10–12	2140–2410	13–39

TABLE 5. ANALYSIS OF SOILS AT *STREPTANTHUS* SITES ON SERPENTINE (n = 22). (Concentrations in $\mu\text{g/g}$ unless otherwise indicated.)

Element	Concentration		
	Lowest	Median	Highest
Al (%)	0.25	1.38	5.46
Ca (%)	0.072	0.426	1.95
Co	85	178	350
Cr	549	1420	3430
Cu	30	45	274
Fe (%)	5.16	9.10	13.8
K (%)	0.026	0.084	0.944
Mg (%)	4.40	15.14	21.25
Mn	711	1304	3420
Na	259	662	8620
Ni	1060	3030	4620
P	115	280	1080
Zn	68	109	265

serpentine soils bioassayed for nickel with *S. polygaloides* had substantial nickel concentrations ($> 1000 \mu\text{g/g}$); the "background" non-serpentine soil had only $52 \mu\text{g/g}$ nickel (Table 6).

Plants of *Streptanthus insignis* from a serpentine locality in the inner South Coast Ranges of California, failed to accumulate significant amounts of nickel when grown on the three serpentine test soils. Nickel values for this serpentine endemic ranged from 15 to $186 \mu\text{g/g}$. This finding substantiates the low nickel values from herbarium samples (Reeves et al. 1981). The other serpentine endemic, *S. barbiger* of the North Coast Ranges, varied widely in its nickel accumulation (Table 7). On one serpentine soil (Newell Mine from Washington State), plants accumulated as much as $1200 \mu\text{g/g}$, and could be classed as a hyperaccumulator species. Yet nickel values ranged from only 69 to $850 \mu\text{g/g}$ on other serpentine test soils. Nickel values from herbarium samples of this species in the 1981 report were even lower ($22\text{--}27 \mu\text{g/g}$). Similar low values were obtained from field-collected *S. barbiger* in 1988 ($4\text{--}21 \mu\text{g/g}$, Table 4). These puzzling results, suggesting incipient capacity for hyperaccumulation by this species, merit further consideration in the Discussion section.

Nickel levels in *S. polygaloides* grown on greenhouse potting mix ($5\text{--}39 \mu\text{g/g}$) can be traced to the storage of nickel in the seed collected on native serpentine soil. The one *Streptanthus* from a non-serpentine habitat, *S. heterophyllus*, failed to grow sufficiently on serpentine for use in chemical analysis.

DISCUSSION

Streptanthus polygaloides. Nearly all tissue samples of *S. polygaloides* proved to have hyperaccumulator levels for nickel (> 1000

TABLE 6. ELEMENT CONCENTRATIONS IN SOILS USED IN GREENHOUSE TESTS. (Concentrations in $\mu\text{g/g}$ unless otherwise indicated.) * See Table 3 for further details.

Soil ^a	Al (%)	Ca (%)	Co	Cr	Cu	Fe (%)	K (%)	Mg (%)	Mn	Na (%)	Ni	P	Zn
1. Serpentine, Hill 1030	0.70	0.224	200	426	30	11.3	0.106	17.9	1610	0.230	3690	617	215
2. Serpentine, talus, Newell Mine	1.58	0.683	118	684	30	5.59	0.100	19.4	1060	0.537	1810	209	93
3. Serpentine, grassland, Newell Mine	3.77	2.300	90	571	25	4.95	0.262	11.4	1070	0.999	1130	481	90
4. Serpentine, Olivine Bridge	0.41	0.259	163	178	19	6.75	<0.022	22.4	1020	0.114	2880	158	96
5. Greenhouse compost/loam	5.29	2.480	19	81	53	2.47	0.673	0.87	636	1.790	52	1940	262

TABLE 7. NICKEL CONCENTRATIONS ($\mu\text{g/g}$) IN *STREPTANTHUS* PLANTS GROWN ON VARIOUS SOILS. ^a *S. heterophyllus* seedlings did not survive on serpentine soils. ^b Maximum value found in herbarium or field specimens (Reeves et al. 1981 and this work).

Soil	Species			
	<i>S. polygaloides</i>	<i>S. barbiger</i>	<i>S. insignis</i>	<i>S. heterophyllus</i> ^a
1. Serpentine, Hill 1030	2110-5460	69-850	55-105	—
2. Serpentine, talus, Newell	1480-2120	550-1200	26-186	—
3. Serpentine, grass, Newell	660-4200	106-456	15-38	—
4. Serpentine, Olivine Bridge	1560-4960	766	18-59	—
5. Greenhouse	5-39	17	3-6	6-7
Field specimens, max. ^b	18,600	27	83	<10

$\mu\text{g/g}$), whether taken from native field sites or when grown in the greenhouse on serpentine soils from localities where *S. polygaloides* is not native. It was not surprising that the one sample of stem tissue (Table 7) contained 660 $\mu\text{g/g}$ of nickel; stems have higher proportions of structural components (cell wall material) and are generally found to have lower nickel concentrations, even in the hyperaccumulator species.

This species, grown on a variety of serpentine soils in the greenhouse had somewhat lower concentrations of nickel (max. of 5460 $\mu\text{g/g}$) than did the field-collected samples. This difference may be a function of differences in plant age and/or mode of growth. In the field, the plants behave as winter annuals, growing as rosettes in the fall and winter, until they bolt in the following spring. During that long growth period, plants in the field can accumulate nickel more or less continuously and thus reach higher concentrations. In contrast, greenhouse plants grow rapidly to maturity in ca. 10 weeks, with less time for nickel uptake. Also greenhouse cultures are afforded optimal conditions for growth (consistent watering, favorable temperatures, etc.).

Other species of Streptanthus. None of the other field-collected serpentine taxa were hyperaccumulators. This was true also for greenhouse-grown *S. insignis*. This confirms the conclusion of Reeves et al. (1981), for results from herbarium samples: Of the several serpentine species of *Streptanthus*, only *S. polygaloides* is a hyperaccumulator of nickel. The one non-serpentine species, *S. heterophyllus*, failed to survive on any serpentine soil. It showed complete intolerance to serpentine conditions, including the high nickel levels.

Streptanthus barbiger. This species grown in the greenhouse on several non-native serpentine soils showed moderate levels of nickel

accumulation, even exceeding 1000 $\mu\text{g/g}$ in one sample (Table 7). *S. barbiger* in the field samples had only low levels of nickel (4-21 $\mu\text{g/g}$, Table 4), and thus acts in the field like a nickel excluder. This surprising result on non-native soils raises the possibility that *S. barbiger* possesses an incipient ability for hyperaccumulation, which may be triggered when grown on non-native serpentine soils, or as well, when growing under greenhouse conditions. This result is all the more curious since *S. insignis*, another serpentine endemic, when grown under similar conditions, does not show any sign of incipient hyperaccumulation.

Although nickel hyperaccumulation is primarily a property of a limited range of serpentine plant species, the degree to which nickel is excluded by normally "non-accumulating" species can sometimes be significantly modified by changes in external conditions, especially soil and climate. Thus a change to another soil (still of ultramafic origin and overall comparable elemental composition) and/or different growth conditions (as in a greenhouse) may provide enough change in factors such as soil pH, Ni availability, soil texture and moisture retention, soil mycorrhizae and diurnal temperature variation, as to lead to considerably increased nickel uptake in some species.

Streptanthus barbiger appears to be an ideal subject for further detailed studies of nickel accumulation. Our research with plants in the field and with plants grown on non-native serpentines, suggests an inherited preadaptation for nickel uptake. It could be that *S. barbiger* has a genetically acquired capacity for nickel uptake, yet has not reached the evolved status of a full-blown hyperaccumulator. A number of approaches present themselves: 1. It may be possible to select for increased nickel accumulation on native or non-native serpentine soils. Individuals with higher nickel levels could be selfed for further selectional response to nickel. 2. Crosses between individuals (intrapopulation or interpopulation) with incipient accumulation capacity could enhance the uptake ability of the progeny. 3. More accessions of population samples of *S. barbiger* could be grown on native and non-native serpentine soils and tested for nickel levels. These trials could be done for plants from both greenhouse culture and plants in the field. In the latter venue, seed of *S. barbiger* could be sown in the field on several serpentine sites where the species is not native. This regime might confirm the potential of *S. barbiger* for nickel accumulation from some serpentine soils, or might indicate that the climatic conditions of the greenhouse are largely responsible for the anomalous behavior observed here.

Evolutionary considerations. We are not unmindful of the evolutionary implications of these results. The most obvious question is why some few serpentine endemics are hyperaccumulators and

others are not; yet still another, *S. barbiger*, may be an incipient accumulator. The related question, equally intriguing, is why most serpentine plants are NOT hyperaccumulators (e.g., exclude nickel).

As a working hypotheses, we propose the following: 1. The nature of the mechanism of hyperaccumulation is idiosyncratic. Each hyperaccumulator, or group of taxonomically related hyperaccumulators can have evolved its own mechanisms for nickel uptake. This seems likely since nickel accumulation occurs in many different and unrelated plants and in many different serpentine environments, tropical to temperate. 2. There may be some degree of genetic preadaptation for nickel accumulation in serpentine tolerant species, as suggested by our findings for *S. barbiger*. Indeed, the early stages of achieving high nickel uptake are likely to involve genotypes preadapted to a modest capability for nickel uptake. One of us (Kruckeberg 1986) has elaborated on the evolutionary sequence for serpentine tolerance by acquiring early, partial preadaptation. The same sequence could apply to the acquisition of a hyperaccumulator genotype.

The most unresolved questions have to do with the evolutionary development of a cellular and molecular basis for nickel accumulation—and for serpentine tolerance in general. What physiological and molecular mechanisms account for this remarkable edaphic capacity? A combination of physiological and molecular biological techniques are needed to solve the fundamental question: How and why does a plant do what it does on serpentine? Alan Baker (1987) has put the research potential well: “. . . metal tolerance [and metal accumulation] in plants will continue to intrigue all those plant scientists attempting to understand the nature and scale of plant adaptations to the environment and will remain an evolutionary paradigm par excellence.”

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ANNOUNCEMENT

NEW PUBLICATION

O'LEARY, J. F., S. A. DESIMONE, D. D. MURPHY, P. F. BRUSSARD, M. S. GILPIN, and R. F. NOSS. 1994. *Bibliographies on Coastal Sage Scrub and Related Malacophyllous Shrublands of Other Mediterranean-Type Climates*. California Wildlife Conservation Bulletin No. 10. 51 p. Contents: Bibliographic sets on various aspects of coastal sage scrub shrublands (e.g., animals; conservation, restoration, and management; fire, diversity, and succession; maps; morphology, phenology, and physiology; soils and water resources; etc.). This is a comprehensive collection of bibliographies regarding an imperiled vegetation type. Copies may be obtained *gratis* from: Kathie Vouchilas, California Department of Fish and Game; 1416 Ninth Street; Sacramento, CA 95814 (916-324-3814) or call California Department of Fish and Game office in San Diego (619-467-4251).